ZOOLOGY.—*A survey of inequivalve pelecypods.* DAVID NICOL, U. S. National Museum.

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In their brief paper on discordant pelecypods Newell and Merchant (1939, p. 176) make the following statement: "Evidently discordancy is not prevalent in modern forms, for there is scarcely any mention of the phenomenon in the literature that we have examined." These authors limit the meaning of discordancy to a difference in height and length measurements of the two valves, or, in their term, the "diameter" of the valves. Although they are correct in implying that little has been written on the subject of discordant valves in modern pelecypods, except in conjunction with general morphologic descriptions of pelecypod taxa, they err in inferring that discordancy is an uncommon phenomenon among living representatives of this class of mollusks.

On page 177, Newell and Merchant make the following statement: "However, there are many modern forms with markedly inequivalve convexity in which the valve margins are perfectly accordant." This certainly is not the case. Most examples of marked inequality of the valve convexities also show some discordancy. Moreover, in some cucullaeids and corbulids, for example, some discordancy is present accompanied by little difference in the convexity of the two valves. Actually, inequal valves of pelecypods may vary as to convesity as well as diameter, and these two variations are sometimes accompanied by a discrepancy in the ornamentation on the two valves of a specimen.

This paper will deal with inequivalve pelecypods in the broader sense because these variations are commonly interrelated morphologically. I have listed in tabular form suborders, superfamilies, families, and genera of inequivalve pelecypods, most of which are also discordant. The list is not to be considered exhaustive, and only a few fossil groups are mentioned. However, from the list alone, it should be quite clear that discordant pelecypods are far from rare.

Many families and genera of normally equivalve pelecypods are, on rare occasions, represented by individuals which, through some freak of growth, whether inspired by environment or by some genetic peculiarity or both, have developed inequal valves. These odd specimens will be ignored for the present discussion. Some of the more unusual occurrences of inequivalve pelecypods are covered by Lamy (1930).

Even in families and genera whose representatives are considered normally equivalve, the two valves usually do not coincide perfectly with each other. A case in point is seen in the Astartidae (Nicol, 1955, p. 155) where in the lunular area the margin of the right valve slightly overlaps the left, whereas in the escutcheonal area the left valve slightly overlaps the right. Cotton and Godfrey (1938, p. 169) point out the same phenomenon in the genus *Cuna* (Crassatellidae). The right valves of some donacids slightly overlap the left valves along the dorsal margin. More examples of this morphologic characteristic could be included. This is apparently a supplementary locking device to keep the valves from twisting, and for our present discussion this phenomenon, with but one possible exception, will not be included in the inequivalve pelecypods.

In this discussion of inequivalve pelecypods I shall begin with the most primitive taxa and conclude with the most specialized ones.

Pelecypods having protobranch ctenidia are structurally the most primitive living members of the class. It is interesting to note that none of them is included in the list of inequivalve forms. Could this mean that the first pelecypods (late Cambrian or early Ordovician) all were equivalve? It may be that the inequivalve characteristic did not appear with the most ancient pelecypods but was a secondary morphologic feature which manifested itself a short time later.

Although the majority of Ordovician pelecypods are equivalve, there are a few genera, most of them having small numbers

of species, which are inequivalve. One such genus is *Aristerella*. It is found in Middle Ordovician strata and is the oldest inequivalve pelecypod I have seen. The exact systematic position of the genus is in doubt; it has been placed among the mytilaceans by most paleontologists and in the pteriaceans by others. Ulrich (1897, p. 524), the original describer, and subsequent workers have reported *Aristerella* as having the right valve larger than the left. This genus has a somewhat pteroid shape, and, if the obliquity of the shell is prosocline, the right valve is the more convex on most, but not all, the specimens examined. (The one or two exceptions are small internal casts and may be examples of distortion.) Two large specimens from Estonia, labeled *Aristerella* in the collection of the U. S. National Museum, are strikingly inequivalve, the right valves being larger than the left. In this respect *Aristerella* is similar to *Heikea* from the late Ordovician of Sweden. Isberg (1934, pp. 273–315, 388–389) describes *Heikea* and allocates the genus to the family Cyrtodontidae, which some systematists have placed among the prionodonts probably for want of a more accurate assignment. Although the specimens which Isberg figures are not markedly inequivalve, he asserts that in most species of *Heikea* the right valves are larger than the left.

Another early Paleozoic group which is inequivalve is the family Antipleuridae. This family of paleoconchs is restricted to the late Silurian and early Devonian and is represented by such genera as *Antipleura*, *Dalila*, and *Dualina*. According to Lamy (1930, p. 130, footnote) either left or right valves may be larger. Figured specimens of these genera show a great difference in the sizes of the valves.

From late Ordovician onward throughout the remainder of the Paleozoic, because of the abundance of pteriaceans and pectinaceans, most of the inequivalve pelecypods have their left valves larger than their right valves. Besides the exceptions to this rule already mentioned, *Vertumnia*, a pterinopectinoid genus restricted to the Devonian; many species of *Cypricardinia*; and the obscure genus *Dexiobia* all have right valves larger than left valves. *Cypricardinia* ranges from Silurian through Mississippian, and *Dexiobia* is confined to the latter Period.

I have not attempted to list all the Paleozoic pelecypods having larger left valves than right. Furthermore, I have listed none in which the inequivalve characteristic is doubtful, whether left or right. Some paleontologists assert that certain Paleozoic genera are inequivalve whereas others do not mention this characteristic in their generic or familial descriptions. The implied discrepancy may be due to oversight on the part of some workers or to distorted specimens in the Paleozoic collections of others.

Bivalves with filibranch ctenidia—i.e., those whose morphological development is second most primitive—constitute the largest group of inequivalve pelecypods from the standpoint of percentage. Most members of this order have well-developed byssal attachments or are attached by their shells directly to the substrate or, if free-living, have descended from ancestors which had some form of attachment. Apparently their pleurothetic mode of life is related to the inequal development of their valves. Furthermore, among the filibranchs, the inequivalve condition is most consistent as well as prevalent. In most families, the inequivalve species always have their left valves larger, but in a few families the inequivalve representatives always have their right valves larger. There are few exceptions, and this consistency can be considered, along with other morphological characters, as an indication of phyletic relationship.

There are several groups of filibranchs which consistently are either equivalve or, if inequivalve, have the left valves larger than the right. The Pteriacea are probably the most ancient and among the most prominent of this group. The Leiopteriidae and Pterineidae commonly have inequal valves, and the left valves are always the larger. (See La Roeque, 1950). A striking example of this inequivalve condition is seen in the genus *Cornellites*. These pteriaceans, which are among the most ancient inequivalve pelecypods, are like the modern species, and it is quite significant that this

large superfamily, which first appeared in the Ordovician Period, has consistently throughout its long history possessed the same inequivalve characteristic—the left valves invariably being the larger. Other fossil pteriaceans which are inequivalve include the genus *Buchia* and the family Myalinidae; both have representatives with their left valves larger than the right. (I must add that I would include the Myalinidae with the Pteriacea rather than the Mytilacea on the bases of the inequivalve condition, the shape of the shell, and the appearance of the ligamental area, despite Newell's assertion in 1942.) Many living species of the Pteriidae are inequivalve, the left valves always being larger than the right.

The mytilaceans seem to be a consistently equivalve group with but few exceptions. *Myoforceps aristata* has prolonged posterior ends of the valves which tend to cross over each other. In some specimens the right and in others the left valves are the larger and more prolonged. Other exceptions are *Stavelia torta* and *Stavelia horrida*, large shells found in the Philippines and Queensland. In these species either right or left valves may be larger. *Fluviolanatus subtorta* is another inequivalve mytilid found in Australian waters.

Another group of filibranchs is the prionodonts, which first appear in the Devonian. The Cucullaeidae and their allies constitute a large suborder, and among its representatives are some species which are inequivalve, the left valves always being the larger and overlapping the right valves along the ventral border. Sometimes this discordancy is accompanied by a striking discrepancy in the ornamentation on the two valves. Some Paleozoic representatives of the Prionodonta and some Paleozoic Pteriacea are remarkably similar in outline and hinge characters, and the fact that both groups have similar inequivalve conditions leads to the possible inference that these two great groups are closely related.

In addition to the pteriaceans and prionodonts, a third and related group having inequivalve species is the Isognomonacea, which includes fossil groups like Cox's Bakevelliidae and the well-known genus *Inoceramus*. Besides the tendency to have inequal valves, the left valves being consistently the larger, these three large groups have other morphologic similarities to link them. The modern isognomonids are not so conspicuously inequivalve as their fossil ancestors, but in an occasional species the larger size of the left valves is noticeable.

The strange family Vulsellidae, which may be related to the isognomonids, has inequivalve representatives. Either valve may be the larger, but the left valve is the larger more commonly than the right. The valves of the vulsellids are often very irregular, but the inequivalve condition is not marked.

In the Placunidae, also, the left valves are commonly larger.

There is some variation as to which valve is the larger in the modern Pectinacea, but in all specimens that are strikingly inequivalve their right valves are the more convex and in most cases overlap the left. The right valves are larger in *Spondylus*, *Plicatula*, *Pedum*, the Cretaceous genus *Neithea*, and some *Pecten*, *sensu lato*. In a few modern pectens, however, the left valves are slightly larger than the right, and this condition is true also in the Propeamussiidae. Newell and Merchant (p. 175) note that the left valves are larger than the right in the late Paleozoic pectinacean genera *Aviculopecten* and *Pernopecten*, but the right valves are larger in specimens of the pterinopectinoid genus *Vertumnia*, which is confined to the Devonian Period. An analysis of the inequivalve condition among the pectinaceans might give some valuable data on the relationships of the many genera and subgenera within the superfamily.

Even a few of the fossil limids are inequivalve. Some Jurassic limids represented in the collection of the U. S. Geological Survey, mainly by those belonging to the genus *Ctenostreon*, have more convex right valves than left. Cox (1943, p. 153) in his description of the family characters of the Limidae made this statement: "There is no anterior subauricular notch like that found in many Pectinidae and Pteriidae, an anterior marginal gape for the protrusion of the foot and byssus affecting (if present) both valves equally." In living species the byssal gape

usually does affect both valves equally, but in some, almost always the strongly-ribbed ones, more of the byssal gape is in the right valve and in a few cases the gape is wholly in the right valve.

In the Ostreidae the left, or attached, valves are either equal in size to, or larger than, the right valves. This is equally true of such Mesozoic genera as *Gryphaea* and *Exogyra* as well as of living species of oysters.

The genus *Chondrodonta*, which is confined to Cretaceous rocks, is attached by its shell to the substrate. Like most ostreids, the attached (left) valves are always the larger. Because of the peculiar hinge and musculature, the systematic position of *Chondrodonta* is still in doubt, and it has been placed in the Ostreidae, Pectinacea, Pinnidae, and Mytilidae by various paleontologists.

On the other hand, the Anomiidae are attached to the substrate by their right valves, but the upper (left) valves are always larger. Likewise, in the aberrant Dimyidae, the left or unattached valves are the larger ones. Two interesting Upper Cretaceous genera, *Diploschiza* and *Pulvinites*, apparently are like *Anomia* and *Dimya* in that they are attached to the substrate by their right valves, and the unattached or upper (left) valves are the larger.

Some aberrant thick-shelled Jurassic and Lower Cretaceous pinnids are inequivalve. These forms are placed in the genera *Trichites* and *Stegoconcha*. In most cases the left valves are the larger.

It is worthwhile to pause here and summarize the data on the filibranchs thus far reviewed. The most noteworthy thing about this large order, with its numerous fossil as well as living representatives, is that the left valves are larger in the preponderance of inequivalve species. The exceptions to this are found in the Paleozoic pectinacean genus *Vertumnia*, most of the Mesozoic and Cenozoic Pectinidae, the Plicatulidae, the Spondylidae, a few of the Vulsellidae, and a few species of the Mytilidae. This, to my mind, has phylogenetic significance and a definite bearing on the classification of the order.

Another characteristic of the filibranchs with a well developed byssus is that where the byssal notch is confined to one valve, or is predominately in one valve, it is the right valve that has the notch or the larger portion of it. This is true of the Pectinacea, Pteriacea, Prionodonta, Anomiidae, Isognomonidae, Limidae (as pointed out previously), and undoubtedly others. I have made only a cursory survey of this characteristic and there may be some exceptions to this condition. However, the character is so consistent among the filibranchs that a definite phyletic unity is indicated. One other observation should be noted here. The pleurothetic filibranchs are more likely to have the byssal notch confined to the right valve. This is not always true, but it is certainly the common condition. On the other hand, some of the prionodonts are attached in a position so that the valve margins are perpendicular to the substrate. In many of these the byssal notch has migrated somewhat so that it is partly in each valve.

Beginning with the Unionacea there are several large families and superfamilies of pelecypods having less primitive ctenidial structure whose representatives, with few exceptions, are equivalve. Some of these exceptions may be unintentionally overlooked, as I have not attempted to trace all aberrant and obscure species of large taxa. Most of the aberrant species occupy a different ecologic niche from the main body of species of a family. Furthermore, in most of these cases either the right or the left valves may be the larger, as typified by *Beguina*, *Miltha*, and a few of the veneraceans.

Among the unionaceans (the Aetheriidae) a few African and South American species are found attached to the substrate by shell cementation. They may be attached by either valve, and either valve may be the larger; furthermore, there is no apparent correlation between which valve is attached and which is the larger. Lamy (pp. 144–151) describes and figures a few contorted and inequivalve specimens of the unionacean genera *Quadrula*, *Unio*, *Pseudospatha*, *Cuneopsis*, *Nodularia*, and *Arconaia*.

The Carditidae are a large and ancient family with nearly all its species equivalve; however, the aberrant genus *Beguina*, which lives in the Indo-Pacific region, is inequivalve, and either valve may be the larger.

Beguina lives surrounded by living coral. Many pelecypods with this type of habitat have either inequal or irregularly-shaped valves.

A few of the dreissenids are discordant, the right valves overlapping the left along a part of the posterior margin.

The inequivalve Rudistacea are among the most bizarre of all pelecypods. This large group of Jurassic and Cretaceous bivalves comprises species attached by either valve and in which either the left valve or the right is the larger. The inequivalve condition in the rudistaceans may be important to point to phyletic relationships within the superfamily.

One of the less primitive families which has very few inequivalve representatives is the Lucinidae. However, among the lucinids the genus *Miltha* has inequivalve species, and either valve may be the larger. Most species of the family Chamidae are also inequivalve, and here again either valve may be the larger. This inequivalve character is one of several indications of the close relationship between the lucinids and the chamids. Among inequivalve specimens of the latter group it is always the attached valves which are the larger.

Even the huge veneracean complex has a few inequivalve species. *Venerupis*, as well as the Petricolidae, have species in which either valve may be slightly larger than the other. In some species of *Claudiconcha* the inequivalve trait is very pronounced, the right valves consistently being the larger. In this connection, incidentally, it is noted that Cotton and Godfrey, in describing the genus, state (p. 248) that the right valve is larger than the left; furthermore, their figure of *Claudiconcha cumingi* (279, p. 247) shows the right overlapping the left, although in their description of this species (p. 249) they assert that the left valve overlaps the right.

Most of the Tellinidae are inequivalve in that the valve margins are sinuous and the posterior side of the shell is commonly bent to the right. In this very large family one finds that either the right valves or the left may be the larger in diameter or the more convex. Within a genus, however, the left or the right valves, as the case may be, are consistently the larger, and, as is the situation in the Pectinidae, a study of the relationships among the inequivalve genera may give some worthwhile suggestions as to the grouping within the family Tellinidae. For a more detailed account of the inequivalve condition in the Tellinidae, see Lamy (pp. 132–134).

A few of the semelids are also inequivalve. The larger number and generally more prominently inequivalve species have the left valves the larger, but in a few cases the right valves may be slightly the more convex. Like the tellinids, the posterior end of the shell is commonly bent, and the direction of bending is usually to the right, rarely to the left. Also like the tellinids, but more prominently and commonly so, the anterior end of the shell is bent in the direction opposite to that of the posterior end.

Most of the Sanguinolariidae are equivalve but a few species are not, the right valves being distinctly larger than the left. Like the Tellinidae, the posterior ends of some species are bent; but unlike the tellinids, they are bent to either the left or the right in about equal numbers.

The description of the inequivalve condition in the tellinids, semelids, and sanguinolariids shows some remarkable similarities and indicates a close relationship of these three families.

Many of the species belonging to the family Pleuromyidae (Triassic to Lower Cretaceous), including those of the genera *Pleuromya*, *Cercomya*, and *Gresslya*, have right valves which overlap the left valves along the dorsal border much like the condition found in some specimens of the Cenozoic family Myidae.

The corbulids are nearly all inequivalve, many markedly so, and the larger valves are invariably the right ones. A few of the related Myidae are also inequivalve, having in all such cases larger right than left valves, furthermore, when the valves of an inequivalve myid are closed the umbo of the right is higher than that of the left.

Among the inequivalve representatives of the lucinids, chamids, veneraceans, tellinids, sanguinolariids, pleuromyids, corbulids, and myids, the larger valves are commonly the right ones; and among those of the four last-named families it is invariably so. This situ-

ation is the opposite of that of the more primitive filibranchs.

The remainder of the pelecypod families discussed are generally inconspicuous groups either because of the small size of the shells or because the groups have small numbers of species and are geographically restricted. In this latter connection, some of the following taxa are not seen frequently because their representatives are restricted to deep water. The relationships of many of these families to each other or to their place in the classification of the Pelecypoda is not well understood. Moreover, their inequivalve condition is not consistent; among the inequivalve species of some families the larger valves are the right, of others they are the left, and of others they may be either one.

The Cleidothaeridae are like chamids in external appearance but are characterized by a pearly inner shell and a very different hinge. This family is confined to Australian and New Zealand waters. Specimens of the one living species are consistently attached by their right valves, which are much larger than their left valves.

In the Myochamidae, representatives of *Myochama* are attached to solid objects by the shells of the right valves, and the left valves are much larger and overlap the right. This condition is much like that found in the Anomiidae. Specimens of *Myodora*, on the other hand, are not attached, and the right valves are always larger, sometimes conspicuously so.

With the possible exception of a species of *Frenamya* which Cotton and Godfrey (p. 145) describe as having the right valves more convex than the left, all of the Pandoridae have the left valves larger than the right, and in some cases the discordancy between the valves is great, the left valves overlapping the right along the ventral border.

The Lyonsiidae are nearly all equivalve, but the few inequivalve species in this family have the left valves larger than the right.

In the Thraciidae the right valves are always larger.

Almost all of the periplomatids are inequivalve, and the larger valves are always the right ones.

Although there is little mention of it in the literature, the Poromyidae are also inequivalve. The right valve of a specimen overlaps the left valve slightly on both the dorsal and the ventral margins.

The Verticordiidae have an unusual type of inequivalve or discordant condition. The right valves overlap the left along the dorsal margin. This morphologic character is similar to that found in the Astartidae and Crassatellidae, but it is much more marked.

Many cuspidariids are inequivalve; the consistently larger left valves overlap the right valves along the posteroventral border.

In some species of Juliidae there are prominent spiral hornlike structures on the umbonal region of the right valves. This morphologic character is unique among the Pelecypoda. A drawing of the structure is given by Cotton and Godfrey (p. 129).

Of the 28 families with living species which are basically inequivalve (this eliminates such groups as the mytilids, carditids, lucinids, and venerids.) half, or 14 of them, have nacreous shells. This is an unusually high percentage as compared with the proportion of nacreous groups in the entire Pelecypoda. Nacreous shells in the Pelecypoda are, in general, considered a primitive characteristic. Whether the relatively high correlation between nacreous shells and inequal valves is significant or not awaits a survey of the nacreous groups in the entire Pelecypoda—a project that is greatly needed.

From the table which summarizes the data and from the more detailed discussion on the various groups, the consistency of the inequivalve trait obviously is important in the classification of the Pelecypoda. Some of the evidence from valve inequality merely substantiates the indications from other morphological characters, but, heretofore, the inequivalve trait has been ignored by taxonomists arranging a classification of the Pelecypoda. To be more specific, the consistently larger left valves found in the Prionodonta, Pteriacea, and Isognomonidae give an indication of relationship which is also borne out by other morphological characters. However, some caution must be exercised as to the interpretation of valve inequality in groups which have few inequivalve species, such as the mytilids and

PELECYPOD TAXA HAVING INEQUIVALVE REPRESENTATIVES

Taxa	The larger valve	
Aristerella		right
Cyrtodontidae[1] (*Heikea*)		right
Antipleuridae	left	right
Cypricardinia		right
Dexiobia		right
Pterineidae	left	
Leiopteriidae	left	
Myalinidae	left	
Pteriidae	left	
Mytilidae[1]	left	right
Prionodonta	left	
Bakevelliidae	left	
Inoceramidae	left	
Isognomonidae	left	
Vulsellidae[1]	left[2]	right
Placunidae	left	
Pectinacea (Paleozoic)	left[2]	right
Pectinacea (Mesozoic, Cenozoic)	left	right[2]
Propeamussiidae	left	
Spondylidae		right
Plicatulidae		right
Limidae[1]		right
Ostreidae	left	
Chondrodonta	left	
Anomiidae	left	
Dimyidae	left	
Pulvinitidae (including *Diploschiza*)	left	
Pinnidae[1] (*Trichites*)	left[2]	right
Unionacea[1] (Aetheriidae)	left	right
Carditidae[1]	left	right
Dreissenidae[1]		right
Rudistacea	left	right
Lucinidae[1]	left	right
Chamidae	left	right
Veneracea[1]	left	right[2]
Tellinidae	left	right
Semelidae	left[2]	right
Sanguinolariidae		right
Pleuromyidae		right
Corbulidae		right
Myidae[1]		right
Cleidothaeridae		right
Myochamidae	left	right
Pandoridae	left	
Lyonsiidae	left	
Thraciidae		right
Periplomatidae		right
Poromyidae		right
Verticordiidae		right
Cuspidariidae	left	
Juliidae		right

[1] Basically equivalve.

[2] Valve which is either more commonly the larger or more conspicuously so or both.

carditids. The few cases of inequal valves in these two groups undoubtedly mean little or nothing as an indication of phyletic relationships.

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